CONTRIBUTION ON THE TAXONOMY OF THE SPINY DOGFISH *SQUALUS ACANTHIAS* L.

by

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ABSTRACT. – Morphometric ratios, such as, pectoral fin-head length, pelvic fin-dorsal fin position and vertebral number do not support the view that there are separate subspecies of *Squalus acanthias*.

RÉSUMÉ. – En étudiant les relations morphométriques telles que longueur de la nageoire pectorale - longueur de la tête, position des nageoires pelviennes - position de la nageoire dorsale, et les variations du nombre de vertèbres, les auteurs concluent à l'absence de sous-espèces chez *Squalus acanthias*.

Key-words : Pisces, Squalidae, Squalus acanthias, morphometry, taxonomy.

INTRODUCTION

Squalus, the type genus of the family Squalidae and the sub-order Squaloidea, is typified by the following characteristics : (1) well developed fin spines lacking lateral grooves, (2) caudal fin without a sub-terminal notch, (3) longitudinal dermal ridges along each side of the caudal peduncle, (4) upper and lower jaws with similar dentition consisting of oblique, sectorial teeth with a single cusp, and (5) typical selachian nostrils without barbels.

A diagnosis of the cosmopolitan genus *Squalus* and its position within the family Squalidae is outlined by Bigelow and Schroeder (1948, 1957) who reviewed the numerous nominal species and separated them into three divisions; (1) *S. acanthias* group, (2) *S. blainvillei* group, (3) *S. megalops-cubensis* group. In his account of the species of *Squalus* from New Zealand and Australia, Garrick (1960) confirmed this grouping. In 1968, Krefft reported that *S. acutipinnis* (Regan, 1908) is associated with the *S. megalops-cubensis* group rather than being synonymous with *S. blainvillei* as had been previously suggested by Bigelow and Schroeder (1948, 1957). In 1973, Merrett gave the name *Squalus asper* to a new species of squalid shark from the equatorial western Indian Ocean. He distinguished this species primarily on the size and shape of the dermal denticles.

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The type specimen designated as *Squalus acanthias* by Linnaeus in 1758 was taken from European waters. Since that time, various stocks from different parts of the world have been found and in some cases assigned different specific and subspecific status. Several authors such as Bigelow and Schroeder (1948), Kato *et al.*, (1967) and Hart (1973) considered the north-eastern Pacific stock (normally inhabiting the continental shelf regions from Baja California to the southern Bering Sea) as belonging to the cosmopolitan species *S. acanthias.* They further proposed that, on the basis of morphometric studies, this stock be accorded a subspecific rank.

Many authors have used morphometric ratios, such as, pectoral-head length ratio, pelvic-dorsal fin position and vertebral number to distinguish between subspecies (Lindberg and Legeza 1956, 1959, Bigelow and Schroeder 1957, Garrick 1960, Springer and Garrick 1964, Forrester 1972, Hart 1973, Jones and Geen 1976).

On the basis of the length of the pectoral fin and the degree of notching of its trailing edge, Lindberg and Legeza (1956, 1959) divided the species into two subspecies, namely, a short-finned *S. acanthias acanthias* with an unnotched or slightly notched edge and a long-finned *S. acanthias suckleyi* with clearly notched fins. These subspecies were found on the east and west coasts of North America respectively. The short-finned type had pectoral fin lengths ranging from 60-90 % (mean 76 %) of distance from the nostril to the last gill slit (pectoral-head length ratio, F: H) and in the long-finned type the figures were 101-110,5 % (mean 106 %). Forrester (1972) agreed with the observations of Lindberg and Legeza and further suggested that dogfish taken off British Columbia were of an intermediate form. Jones and Geen (1976) stated that the F:H ratio for animals from the Straits of Georgia produced significant positive regressions when plotted against length. However, they pointed out that this was only true for reproductively immature animals, and further that the ratio varied according to the method of preservation. Data on the position of the pelvic fins relative to the dorsals ($P\text{-}D_2 : D_1\text{-}P$ ratio) in specimens from the Straits of Georgia indicated that the pelvic fins are closer to the second dorsal than to the first (Jones and Geen 1976a). Bigelow and Schroeder (1957) and Garrick (1960) reported that the pelvic fins in the *S. acanthias* group were about midway between a perpendicular at the point of emergence of 2nd dorsal spine and one at the free rear tip of 1st dorsal fin. However, in juveniles and half-grown specimens, Garrick reported that the pelvic fins were nearer to a perpendicular at the posterior tip of the 1st dorsal fin than to one at the exposed origin of the 2nd dorsal spine. For the *S. blainvillei* group and *S. megalops-cubensis* group these two authors agreed that the pelvic fins were nearer to a perpendicular at the posterior tip of the 1st dorsal than to one at the exposed origin of the 2nd dorsal spine, and hence resembled immature *S. acanthias.* This confirmed the observation reported by Lindberg and Legeza (1956) for the *S. megalops-cubensis* group. Garrick also stated that the dimensional feature most affected by growth is the position of the pelvic fin relatively to the dorsal fins and any expression of this will need qualification to cover at least small and large specimens. Jones and Geen (1976) confirmed this and stated that the differences reported above may have resulted from the effects of length and sex.

Other characteristics which have been used to distinguish between species of dogfish, especially those from the North East Pacific and the Atlantic, are vertebral numbers. However, Jones and Geen (1976) stated that subspecific designations on the basis of vertebral numbers are not appropriate.

At the present time there seems to be no evidence, either from morphometric or biochemical studies on muscle protein and blood haemoglobins (see Jones and Geen 1976), that there are subspecies of *S. acanthias* and hence there is general agreement with Bailey *et al.* (1970) on the undivided taxonomic status of this species.

MATERIAL AND METHODS

Material was collected in 1976-1980 from Whitehaven and Bangor, U.K., and consisted of 191 specimens of the spiny dogfish, *Squalus acanthias,* of which 110 were males and 81 females. The males varied in length from 22.1 to 84.9 cm and the sample included 16 embryos which were between 22.1 and 22.5 cm. The females measured 22.4 to 99.9 cm in length and included 12 embryos from 22.4 to 24.6 cm.

The following measurements were taken (see Fig. 1) :

L, total length from tip of the snout to limit of the caudal fin when depressed to align with body axis.

H, distance from middle of nostril to last gill slit.

F, length of the pectoral fin to its origin at the 5th gill slit.

D_1-P, length from the posterior limit of the base of first dorsal fin to a similar position on the pelvic fin.

P-D_2, distance from the posterior limit of the base of the pelvic fin to a similar position on the second dorsal fin.

Vertebrae from 66 males (length 49.80 to 84.98 cm) and 49 females (49.47 to 99.37 cm) were counted by removing the soft tissues ventral to the vertebral column. This proved an effective method for such counts and avoided the necessity for making X-ray photographs.

Each vertebrae count was separated into two parts :

(a) Precaudal vertebrae (PCV), including all centra anterior to the forward edge of the precaudal pit (see Fig. 1).

(b) Caudal vertebrae (CV), all centra posterior to the precaudal pit.

It is necessary to use a dissecting microscope to count the last few caudal vertebrae.

Cumulative percentage length-frequency plots were made on arithmetic probability paper. This method of Harding (1949) later modified by Cassie (1954) identifies heterogeneity, since a normally distributed population generates a straight

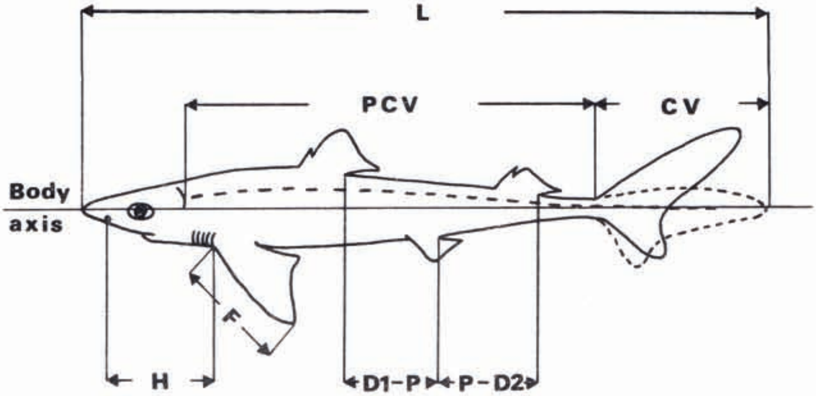

Fig. 1. – *S. acanthias*, morphometric measurements. D_1-P, length from the posterior limit of the base of the first dorsal fin to a similar position on the pelvic fin; P-D_2, distance from the posterior limit of the base of the pelvic fin to a similar position on the second dorsal fin; F, length of the pectoral fin from its origin at the 5th gill slit; H, distance from middle of nostril to the last gill slit; L, total length; CV, caudal vertebrae; PCV, precaudal vertebrae.

line. However, a sample containing two sub-samples gives a bimodal curve, and the curve from a population of sub-samples is polymodal. The Cassie method also allows an estimate of the mean and standard deviation of each sample or sub-sample to be calculated directly.

For the purpose in this study all male and female embryos were omitted for the age-determination.

RESULTS

Analysis of males

The graphical method of Cassie (1954) was used to analyse the distribution within a sample population of *S. scanthias*. In order to make some estimate of the age of the fish in the various size groups, the growth curves presented by Holden and Meadows (1962) were used (see Fig. 2) rather than direct estimations of age from examination of rings on the centrum or the number of spine markings (see discussion). Fig. 3 is Cassie curves, for 94 males ranging in length from 49 to 85 cm. Although it is difficult to accurately fix the points at which the various sub-groups separate, it is clear that the sample contained individuals belonging to a number of size and hence probably age groups. These are summarized in Table I .

TABLE I. – Size groups of male *S. acanthias*.

Group	Length (cm)	Mean length (cm)	Approximate age in years
1	50 - 61	55.09 ∓ 3.47	2.8 - 4.7
2	62 - 68	65 ∓ 2.16	5 - 7
3	69 - 85	75.71 ∓ 4.59	7.5

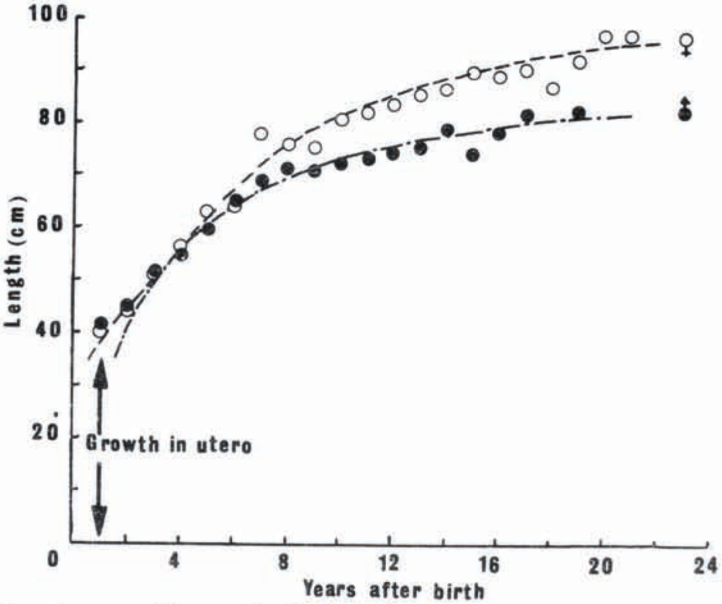

Fig. 2.– Growth curves of *S. acanthias*. Re-drawn from Holden and Meadows (1962).

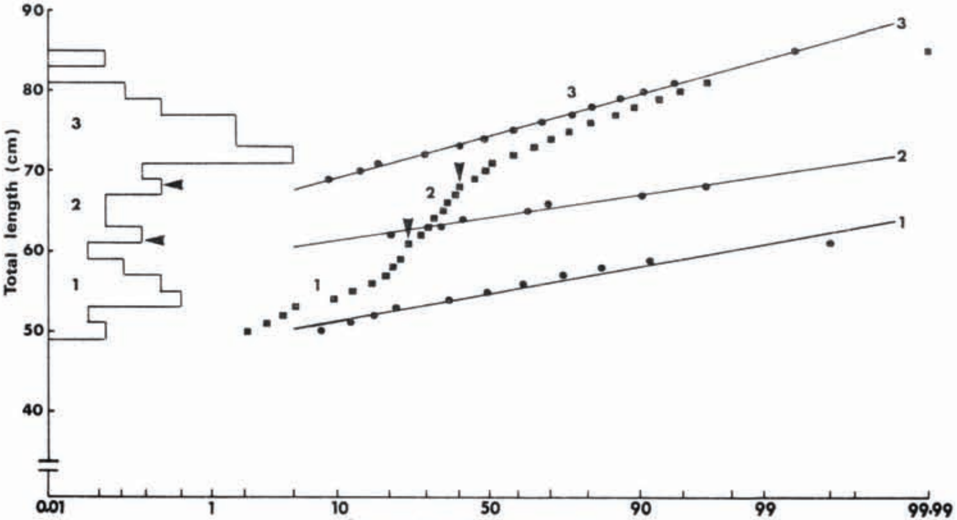

Fig. 3.– Cassie curve for a sample of 94 male *S. acanthias*. The continuous curve (blocks) represents the percentage cumulative frequency of the whole sample, and the oblique straight lines the percentage cumulative frequency in each size group. Arrow ( ) indicate points chosen as dividing the successive size groups. The size frequency distribution of the sample is illustrated by an histogram.

Analysis of females

Fig. 4 is Cassie curves for 69 females from 48 to 100 cm in length. Examination of the graphs shows that as in the males, the sample contained a number of sub-populations (see Table II).

TABLE II. – Size groups of female *S. acanthias.*

Group	Length (cm)	Mean length (cm)	Approximate age in years
1	50 - 54	52.25 ∓ 1.70	2.6 - 3.3
2	55 - 62	58.5 ∓ 2.44	3.5 - 4.8
3	63 - 73	69 ∓ 3.20	4.9 - 7.3
4	74 - 84	78.77 ∓ 3.63	7.6 - 11.5
5	85 - 100	92.75 ∓ 4.59	12

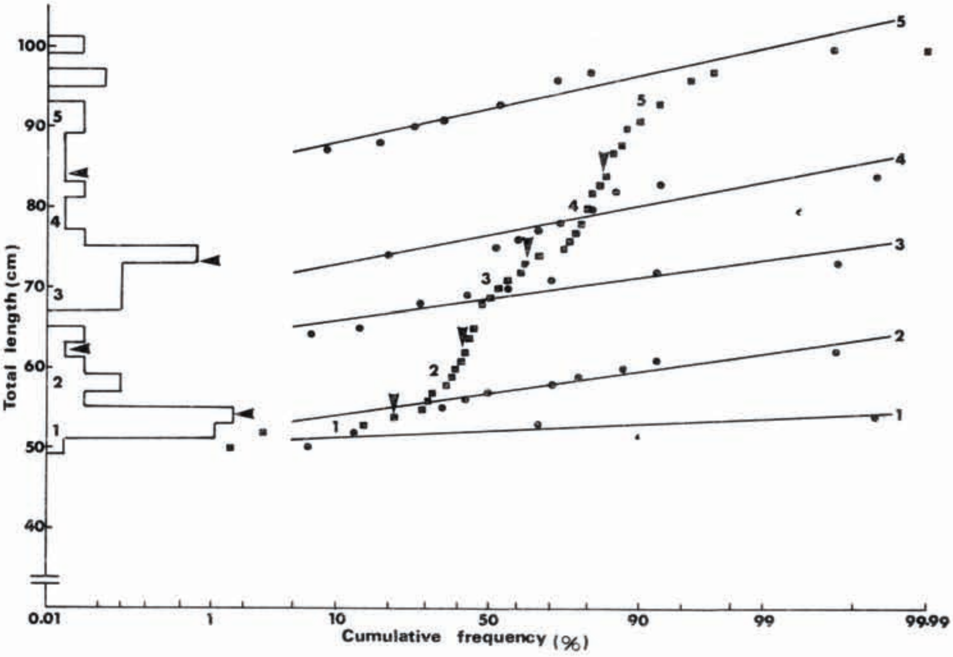

Fig. 4.– Cassie curve for 69 female *S. acanthias.* The continuous curve (blocks) represents the percentage cumulative frequency of the whole sample, and the oblique straight lines the percentage cumulative frequency in each size group. Arrows (.) indicate points chosen as dividing the successive groups. The size frequency distribution of the sample is illustrated by an histogram.

Pectoral fin-head length ratio.

The length of the pectoral fin exceeded the head length in only one male measuring 53.25 cm and equalled the head length in a single 71.05 cm male and a female 90.8 cm in length. In all other cases the length of the head exceeded that of the fin and the ratio of pectoral fin (F) to head length (H) was plotted against total body length (L) and the regression lines calculated (see Figs 5, 6, 7 and 8). Immature males showed a significant positive slope, $r = 0.86$; $p < 0.001$ with 47 degrees of freedom and the values for immature females were, $r = 0.78$; $p < 0.001$ with 66 degrees of freedom (Figs 5 and 6). The F:H ratio data for mature individuals showed no correlation with length ($r = 0.19$; $p > 0.1$ with 61 degrees of freedom in the case of the male and $r = 0.35$; $p > 0.1$ with 13 degrees of freedom for the females (see Figs 7, 8 and Table III).

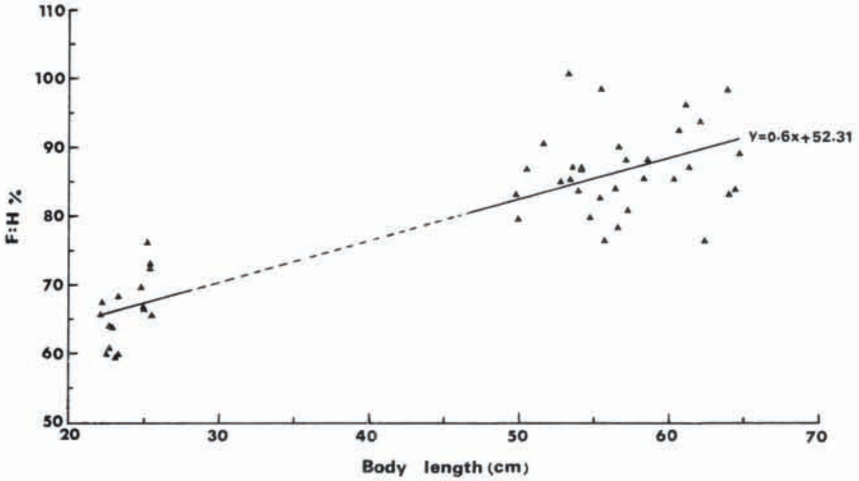

Fig. 5.– Relationship of relative length of pectoral fin to head and total body length for *S. acanthias*, immature males.

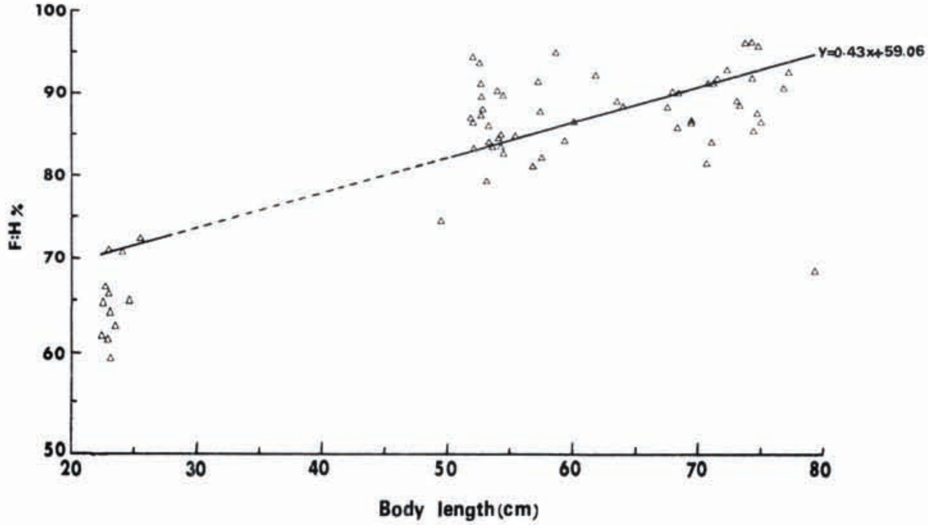

Fig. 6.– Relationship of relative length of pectoral fin to head and total body length for *S. acanthias*, immature females.

TABLE III. – Summary of data showing the relation between the total body length to F:H ratio for *S. acanthias*. (r : correlation coefficient of regression F: H-L; N : number sampled; L : total body length; p : probability).

Sex	N	age (years)	L (cm)	F:H (%)	r	p
Male						
immature	48	up to 5.5	22.1 - 64.7	59.5 - 100.89	0.8622	$<$ 0.001
mature	62	6	65.65 - 84.98	100 - 72.59	– 0.195	$>$ 0.1
Female						
immature	67	up to 9.2	22.4 - 79.3	59.52 - 94.65	0.7803	$<$ 0.001
mature	14	10	81.44 - 99.9	84.95 - 100	0.3505	$>$ 0.1

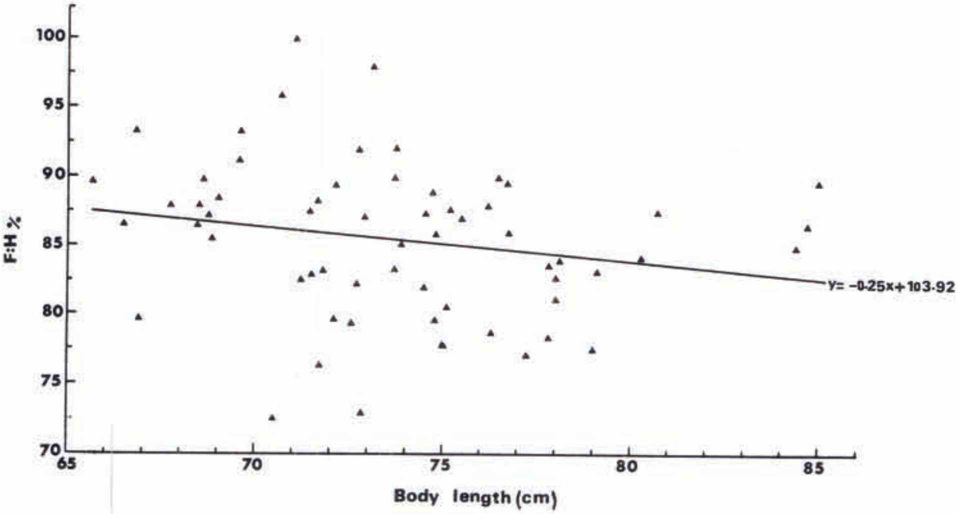

Fig. 7.– Relationship of relative length of pectoral fin to head and total body length for *S. acanthias*, mature males.

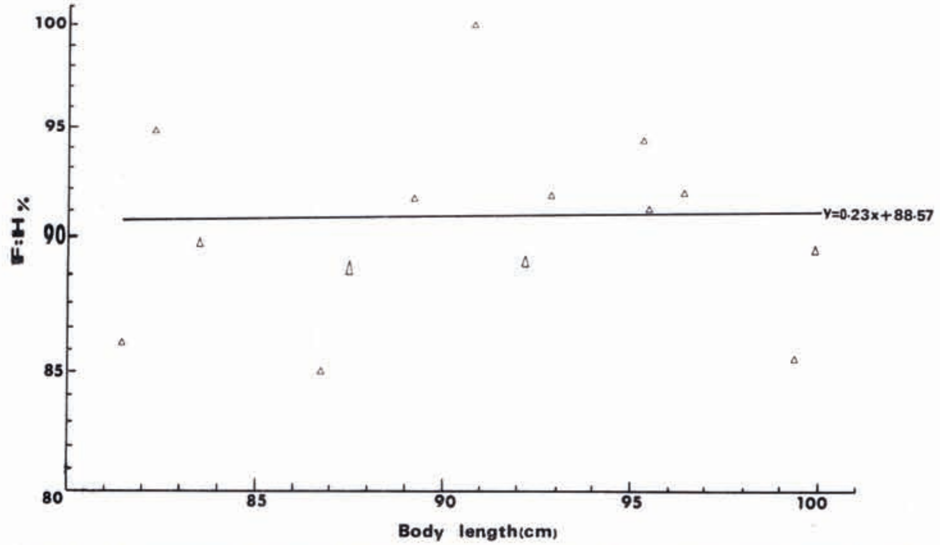

Fig. 8.– Relationship of relative length of pectoral fin to head and total body length for *S. acanthias*, mature females.

Forrester (1972) found the regressions of relative fin length against body length for males and females of dogfish from Queen Charlotte Sound (Pacific Ocean), and the Strait of Georgia showed a significant ($p = 0.05$) positive slope in all cases. However, the results from our study agree with those of Jones and Geen (1976) who used samples from the Straits of Georgia (see Table IV). They concluded that in their material, the F:H ratio showed a significant ($p = 0.05$) positive regression on length for reproductively immature animals, but not for transitional and mature ones.

TABLE IV. – Comparison between total body length and the ratio pectoral fin length/head (F:H ratio) for *S. acanthias* from British Columbian waters (after Jones and Geen 1976).

Area, source, sex	N	L (cm)	F:H ratio (%)
Jones and Geen (1976)	Strait of Georgia		
Males (immature)	46	25.3 - 69.4	57.1 - 91.5
(transitional and mature)	27	71.8 - 97.8	84.4 - 97.2
Females (immature)	68	24.3 - 94.5	54.2 - 98.6
(transitional and mature)	32	78.3 - 122.5	80.6 - 104.3
Forrester (1972)			
Males	168	71.6 - 91.5	81.8 - 100
Females	33	72.6 - 113.5	85.2 - 100
	Queen Charlotte Sound		
Forrester (1972			
Males	51	48.0 - 89.8	73.9 - 97.8
Females	51	47.6 - 111.7	74.8 - 95.7

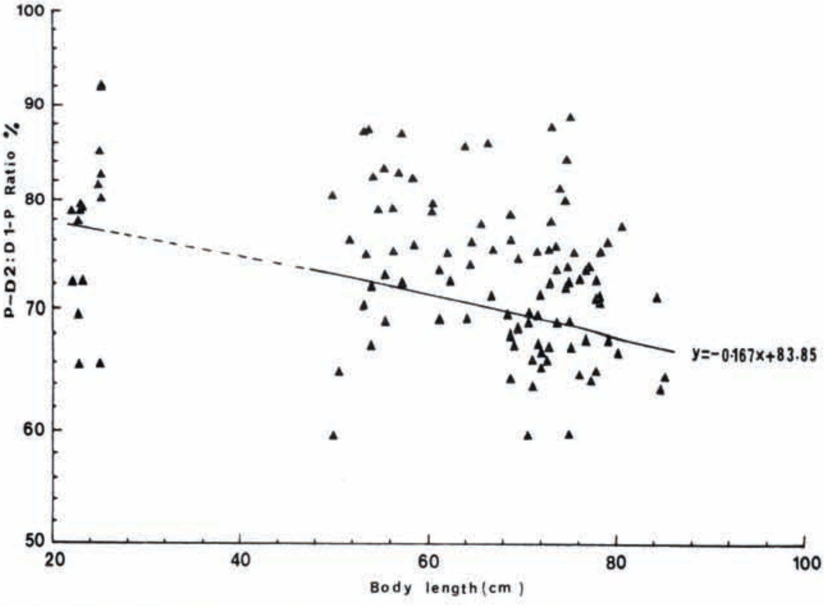

Fig. 9.– Relation of relative position of pelvic fins to dorsal fins and total body length for *S. acanthias*, males.

Pelvic-dorsal fin position

The data shown in Figures 9 and 10 indicate that the pelvic fins are closer to the second dorsal than the first. The P-D$_2$:D$_1$-P ratio data has a significant negative regression on length, $r = 0.36$, $p < 0.001$ with 109 degrees of freedom for males, and $r = -0.56$, $p < 0.001$ with 80 degrees of freedom for females. These results agree with those of Jones and Geen (1976) who stated that the P-D$_2$: D$_1$-P ratio has a significant ($p < 0.05$) negative regression on length (for the samples from the Straits of Georgia and North Pacific dogfish stocks, see also Table V).

TABLE V. – Summary of present findings and those of Lindberg and Legeza (1956), Bigelow and Schroeder (1957), Garrick (1960) and Jones and Geen (1976).

Group, source, sex	N	L (cm)	P-D$_2$: D$_1$-P ratio (%)
S. acanthias			
Jones and Geen (1976a) males	80	25.3 - 97.8	92.1 - 54.8
females	102	24.3 - 122.5	78.7 - 45.6
Bigelow and Schroeder (1957)	–	–	⩾ 100
Garrick (1960)	8	23 - 99	293 - 80
S. blainvillei			
Bigelow and Schroeder (1957)	–	–	< 100
Garrick (1960)	6	21 - 98	327 - 152
S. megalops-cubensis			
Lindberg and Legeza (1956)	–	–	126
Bigelow and Schroeder (1957)	–	–	> 100
S. acanthias			
Present study males	110	22.1 - 84.98	96.44 - 38.99
females	81	22.4 - 99.9	83.30 - 51.25

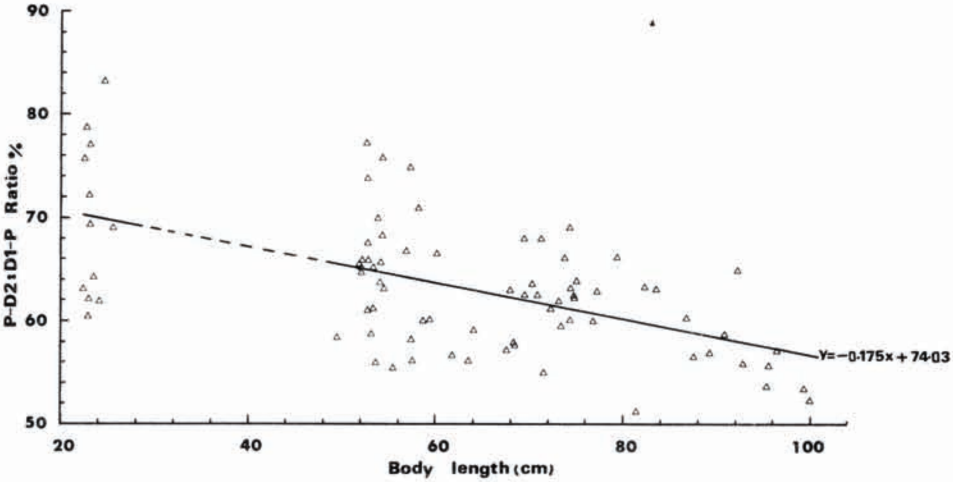

Fig. 10.– Relation of relative position of pelvic fins to dorsal fins and total body length for *S. acanthias*, females.

Total vertebral number

The other character which has been used to distinguish the supposed North-eastern Pacific subspecies of *S. acanthias* from the Atlantic form is the vertebral number. Data from this study indicate that there is no variation in vertebral counts in males and females and is summarized in Table VI and fig. 11. Our data again support those of Jones and Geen's sample from the East coast of North America, but not those from the West coast.

TABLE VI. – Vertebral numbers of *S. acanthias* stocks.

Stocks		Total vertebral No.	
	N	Mean	Standard deviation
East coast of North America	20	112.5	2.70
S. South America	5	105.8	2.59
West coast of North America	47	100.3	2.67
Present study	115	112.5	2.1

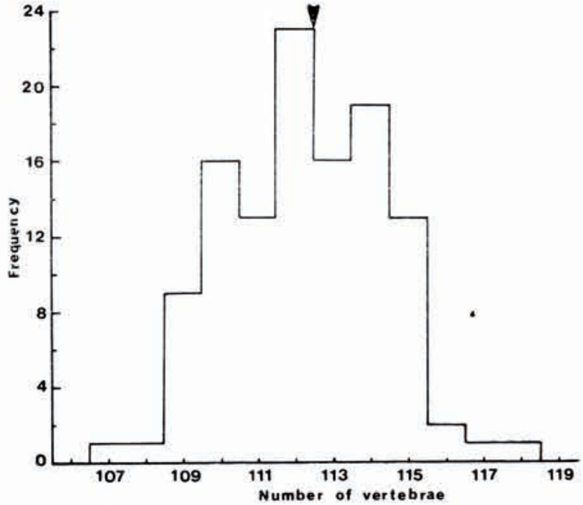

Fig. 11.– Vertebral number frequency for *S. acanthias*. Arrow indicates the mean vertebral number.

DISCUSSION

Elasmobranch fishes cannot be aged by scale or otolith readings and hence alternative methods of age determination have been utilized. These include tagging data (Templeman 1958, 1976; Holden 1967), size frequencies (Olsen 1954, Aasen 1966), spine readings (Holden and Meadows 1962; Ketchen 1975), tooth-replacement rates (Moss 1967, 1972) and observations of the vertebral centrum (Daiber 1960; Taylor and Holden 1964; Stevens 1975; Jones and Geen 1977 and Tanaka and Mizue 1979). Most of these methods are time consuming, relatively inaccurate and generally difficult to apply. In particular the rings which have been used for age determination, cannot be shown to be annual and hence all previous workers have experienced problems.

In the present study, ageing of *S. acanthias* was attempted using the markings on the second dorsal spine and the rings on the vertebrae, but the problems, confronted by other authors, remained the same. Therefore, graphical methods of separating age groups devised by Harding (1949) and Cassie (1954) were used and the age estimations were related to those of Holden and Meadows (1962).

Although Cassie's method provides a useful way of distinguishing groups within a population, it is best carried out with some independent estimate of the number in each age group and mean lengths (Mathews 1974). Also, Cassie curves are sensitive to slight changes in the location of the dividing line between age groups and any deviations from normality in distribution, both of which could cause major differences in interpretation (Mathews 1974).

Little is known about the early growth of *S. acanthias* since small fish are generally absent from catches using small-mesh bottom trawls (Ketchen, 1975). There were no small *S. acanthias* in samples used in the present study; this may be explained by the preference of small fish for shallow waters which are better suited to their feeding (Hickling 1930).

As indicated above, there has been considerable discussion on the specific status of the different stocks of *S. acanthias*. Such discussion have largely involved morphometric measurements, such as F:H ratio, P-D_2: D_1-P ratio and vertebral number.

The existence of two subspecies of *S. acanthias* in the northern hemisphere has been suggested by Lindberg and Legeza (1959) on the basis of the length of the anterior pectoral margin compared with the distance from the 5th gill-slit to the centre of the nostril. They recognised *S. acanthias acanthias* as a short-finned form and *S. acanthias suckleyi* as a long-finned one. These subspecies occur in the east and west coasts of North America respectively.

Special significance has been attached to the number of vertebrae in the proposed subspecies. In the material used in the present study, the vertebral number is 112.5 ± 2.1, which agrees with that of Jones and Geen's samples from the East coast of North America, but not those from the West. However, Jones and Geen (1976) stated that the vertebral number of dogfish from the East and West coast, are significantly different and a southeastern Pacific stock have vertebral numbers somewhat intermediate between these groups.

Mayr (1969) points out that if data ranges for particular characteristics, such as vertebral numbers, overlap between supposedly discontinuous stocks by more than 20%, then by convention they do not warrant subspecific recognition. Jones and Geen (1976) reported that the overlap is 29 % between the northeastern and southern Pacific stocks, and 21 % between this latter stock and the Northwestern Atlantic stock and they concluded that subspecific designations for the northeastern Pacific dogfish and for the Atlantic form, on the basis of vertebral numbers, is inappropriate.

Finally, Jones and Geen (1976) cast some doubt on the value of morphometric ratios to distinguish between subspecies and species groups respectively because of the environmental and preservational influences. In addition, they stated that the pattern of dogfish migration between Scotland, the Barents Sea, Newfoundland, Iceland and from Washington to Japan which has been described by Anon. (1952), Templeman (1958), Aasen (1962) and Holden (1967) might be of considerable importance. In addition, Templeman (1976) reported the first record of a west to east transatlantic migration of tagged spiny dogfish and concluded that while transatlantic migration is not great but probably not highly unusual (Fig. 12). Therefore, consequent interbreeding would tend to eliminate morphometric differences. Jones and Geen (1976) also pointed out that electrophoretic analysis of muscle proteins suggested that separation into subspecies was not warranted. This study does not support the view that there are subspecies of *S. acanthias.*

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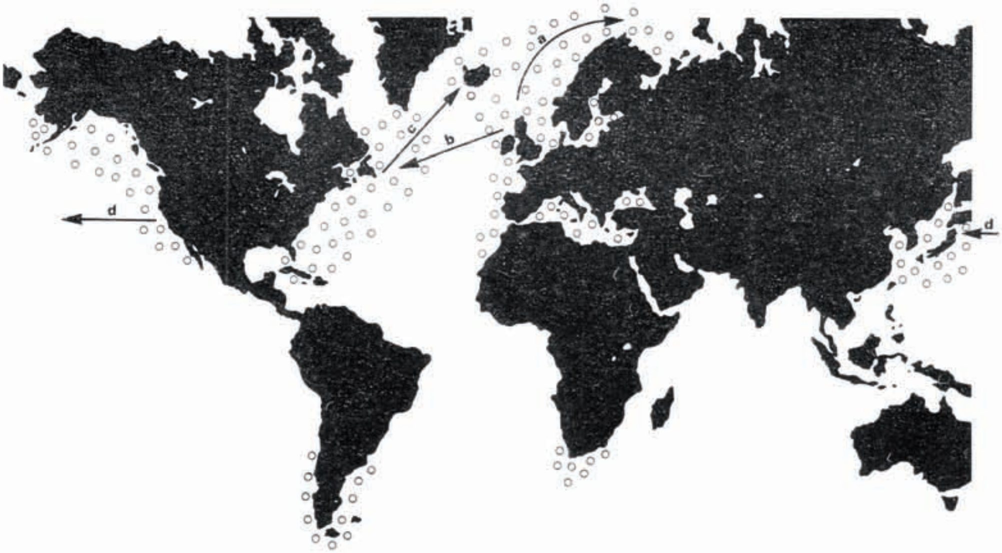

Fig. 12.– Global distribution of *S. acanthias* (circles). After, Bigelow and Schroeder (1957), Lindberg and Legeza (1956), Springer and Garrick (1964), and Hart (1973). Arrows indicate movements of dogfish between stocks determined by tagging studies. a, Scotland to Barents Sea (Aasen 1962); b, Scotland to Newfoundland (Holden 1967b); c, Newfoundland to Iceland (Templeman 1958); and d, Washington to Japan (Anon, 1952).

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